ACTINOPTERYGIANS FROM THE EARLY TRIASSIC ARCADIA FORMATION, QUEENSLAND, AUSTRALIA

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Isolated scales and small patches of articulated scales, collected as surface scrap, provide evidence of 6 additional types of actinopterygian from the Arcadia Formation. Prior to the description of these scales, *Saurichthys* was the only actinopterygian known from the Arcadia Formation and as none of the scales are referable to this genus, they significantly increase the faunal diversity of the collections. ❒ *Actinopterygians, Arcadia Formation, Queensland, Australia.*

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Exposures of the Arcadia Formation are seldom fossiliferous but there are two localities where the sediments erode to form natural craters in which vertebrate fossils become concentrated. Assemblages accumulated over a 30-year period, mostly of surface scrap, are dominated by the remains of temnospondyl amphibians, with procolophonids, basal archosaurs and other small reptiles present in small but significant numbers. Lungfish toothplates are also common. Actinopterygian remains are rare, except as inclusions in coprolites, which occur in abundance (Northwood, 1997). The only actinopterygian previously recorded from the assemblages is *Saurichthys* cf *S. gigas* (Turner, 1982).

It is clear from the frequency of coprolites containing scales that actinopterygians were important members of the community represented in the Arcadia Formation. Unfortunately, most of the scales in the coprolites are too poorly preserved to be described. Instead, an idea of the diversity of actinopterygians present can be gained by studying scales preserved in small pieces of matrix collected with the surface scrap. Some of these scales are reasonably well preserved and remain articulated. Others are scattered through small pieces of fine sandstone or mudstone and vary in their quality of preservation. Variations in morphology and surface ornamentation allow different types of actinopterygians to be recognised.

The scales described here are from two sites, Queensland Museum Locality (QML) 78 (the Crater), which lies approximately 72km SW of Rolleston, and QML215 (Duckworth Creek), situated SW of Bluff, both in S central Queensland, and approximately 175km NNE of QML78. Sediments at the two localities are derived from high-sinuosity, meandering to anastomosing streams subject to frequent seasonal flooding. Thick successions of massive purplish-red overbank mudstones enclose well defined channel sandstones which are whitish-green, fine to medium grained, and cross-bedded. Channel deposits are more abundant at QML215 than at QML78. Flash floods are represented by thin bands of massive to weakly laminated, whitish-green mudstone and very fine sandstone interbedded with red mudstone. Vertebrate fossils are recovered mostly from the fine grained sediments, but isolated elements are recovered occasionally from the more coarse grained sandstone. Most of the actinopterygian scales are enclosed in fine to medium-grained red matrix, which suggests preservation in interchannel mudstones, probably on mud flats. At QML215 some specimens are preserved in green mudstone thought to have been deposited in a swampy environment (Northwood, 1997).

Scales described in this paper are divided into six types representing different actinopterygian taxa, all of which are new for the Arcadia Formation. Comparisons are made with scales from other Early Triassic actinopterygians from Australia and South Africa. Two main problems were encountered during this analysis. First, there seems to be a preservational bias against fish in most Early Triassic non-marine deposits that limits the available comparative material. Secondly, the scales of those actinopterygians which are known from the Early Triassic are incompletely preserved or not described in detail.

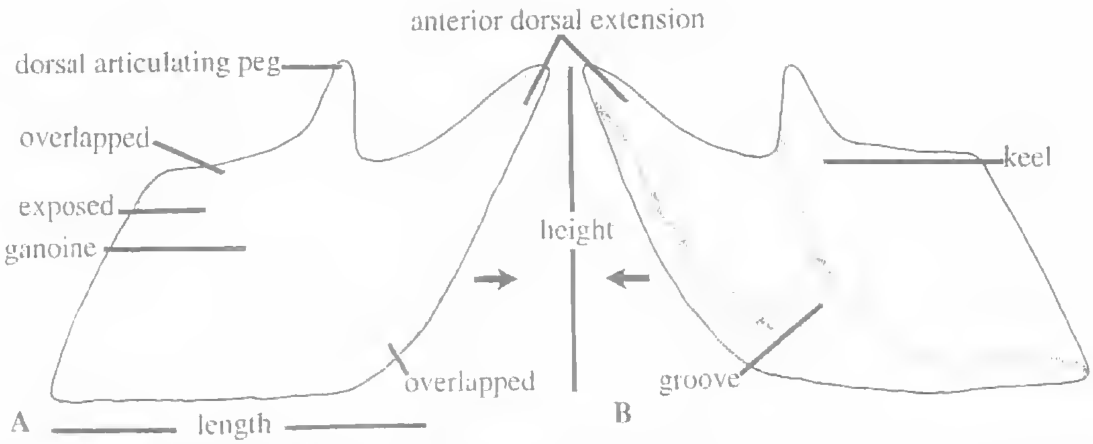

FIG. 1. Morphological features of Early Triassic actinopterygian scales and the terminology used to describe them. A, external view; B, internal view; arrow = anterior.

The Australian actinopterygians are no exception. Despite these problems, the comparisons indicate that some of the Arcadia scales may belong to members of the Acrolepidae and Perleididae.

MORPHOLOGICAL CHARACTERISTICS OF ACTINOPTERYGIAN SCALES

Characteristically, most Early Triassic actinopterygians have ossified scales with thick laminated ganoine on their exposed surface. The morphological features of actinopterygian scales and the terminology used here to describe them are shown in Figure 1.

The scales of early actinopterygians differ in morphology according to body region (Fig. 2). In general, the scales decrease in height and increase in length toward the caudal, ventral and dorsal regions of the body (Esin, 1990). In the mid-lateral area, the scales are quadrangular, and those nearer the tail are more diamond shaped and less overlapped. Peg-and-groove articulation is reduced or absent in the posterior body scales. Ventral scales tend to be narrow and elongated with a large overlapped area anteriorly (Esin, 1990). This morphological variation of body scales is not great enough to allow the different types of scales from the Arcadia Formation to be from a single taxon.

Esin (1990) observed that other difficulties with using isolated scales for taxonomic purposes are that scales change during ontogeny, and that there is substantial parallelism in the scale morphology of various groups of actinopterygians.

DESCRIPTION

TYPE 1.

MATERIAL. QMF35237 (Fig. 3), a single posterior flank scale, preserved in external view in consolidated red mudstone. Locality. QML215.

Scale type 1 is delicate, with a smoothed rhombic shape (Fig. 3). It has a prominent dorsal peg and the anterodorsal corner of the scale extends dorsally beyond the peg. The ganoine layer is thin and the scale is not ornamented. The height and length of the scale are roughly equivalent

TYPE 2.

MATERIAL. QMF35238 (Fig. 4A,B,C), anterior - mid lateral body scales, some of which remain articulated, in a small block of red mudstone. Locality. QML215.

Material probably referrable to type 2: QMF35251 from QML215 and QMF35252 from QML78.

Type 2 scales are large, thick, and robust (Fig. 4). The external surface is unornamented and is covered with thick multi-layered ganoine. Dorsally, a prominent peg articulates with a deep ventral groove in the adjoining scale (Fig. 4B,C). Scale type 2 has an extension of the anterodorsal corner, similar to that of scale type 1. On the internal surface of the scale, there is an obvious keel and a depressed area into which the anterodorsal extension of the adjacent scale fits (Fig. 4B). Similar scales have been found at both QML215 and QML78 but are not so well preserved.

TYPE 3.

MATERIAL. QMF35239 (Fig. 5A), articulated caudal scales, including the lateral line series, in red mudstone.

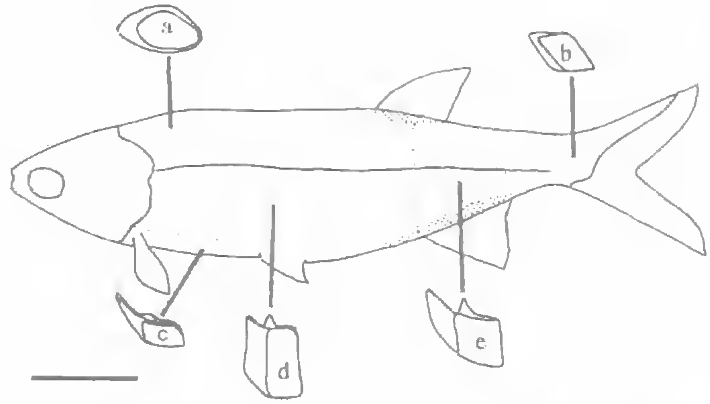

FIG. 2. Morphological variation of scales in the body of a generalised Early Triassic actinopterygian. Dot-shaded areas sometimes have specialised scales, but these were not included as they vary in form between different actinopterygians with less consistency than the other body scales. Scales are adapted from Esin (1990), who figured scales from the different body regions of *Amblypterina costata*. a = anterior dorsal scale, b = caudal scale, c = anterior ventral scale, d = lateral scale, e = posterior flank scale. Scalebar a-e = 5mm; outline of the fish is not drawn to scale.

Only the external surface is exposed. Additional material: QMF35253 (Fig. 5B), scales and lepidotrichia scattered throughout a block of red mudstone that may be a partly decomposed coprolite. Locality. QML78.

The external surface of scale type 3 is ornamented with 3 - 4 rugae that run diagonally across the scale from below the anterodorsal corner to the posteroventral corner (Fig. 5A). There is a slight extension of the anterodorsal corner of the scale which gives it a leaf-like shape. It is a very small, delicate scale with no articulating peg or groove. Often, only the trunk scales of Early Triassic actinopterygians are connected by a peg-and-groove arrangement and the absence of these features in scale type 3 may simply reflect the posterior body position of the scales. The internal surface of scale type 3 has a slight keel and a marginally depressed area where the adjacent scale overlapped (Fig. 5B). Articulated scales show only a slight degree of imbrication.

TYPE 4.

MATERIAL. QMF35240 (Fig. 6A), articulated mid-body scales, including the lateral line series, in a small block of red mudstone. Locality. QML78. Additional Material: QMF35254, 35255, 35256 from QML78 and QMF35257, 35258 (Fig. 6B,C) and 35259 from QML215. At QML78 the scales occur in pieces of consolidated red mudstone with one, QMF35256, occurring in green mudstone.

The actinopterygian represented by scale type 4 is characterised by lateral body scales that are at least 3 times greater in height than length (Fig. 6). The lateral-line crosses the upper quarter of the scales obliquely (Fig. 6A,C). Unlike most of the scale types, type 4 has been collected at both localities, and occurs only as articulated patches of scales. Most of the type 4 scales are poorly preserved and often only the ganoine layer remains. Thus it is unknown whether these scales have a peg-and-groove articulation

Type 4 scales from L215 are less well preserved than those from QML78 and most are little more than impressions in green mudstone. Some of the specimens from QML215 include fin lepidotrichia and lateral-line scales (Fig. 6B,C). Others include the dorsal and ventral margins of the body, where the elongated flank scales grade into smaller, rhombic scales.

TYPE 5.

MATERIAL. QMF35241 (Fig. 7), an articulated patch of mid-posterior flank scales, including the lateral line series, in consolidated red mudstone. Additional material. QMF35260. Locality. QML215.

Type 5 scales are rhombic with no evidence of a peg-and-groove articulation (Fig. 7). In general, the height of the scales is slightly greater than their length (Fig.7A), except for the lateral-line scales which are twice as high as they are long (Fig. 7B). The lateral-line scales have a characteristic notch in the posterior edge and a

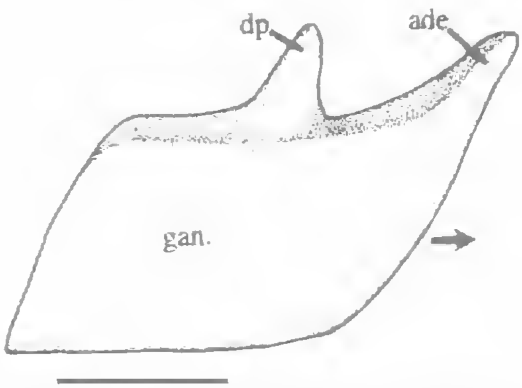

FIG. 3. Scale type 1, QMF35237, posterior flank scale in external view. ade = anterodorsal extension, dp = dorsal peg, gan. = ganoine, Arrow = anterior. Scalebar = 1mm.

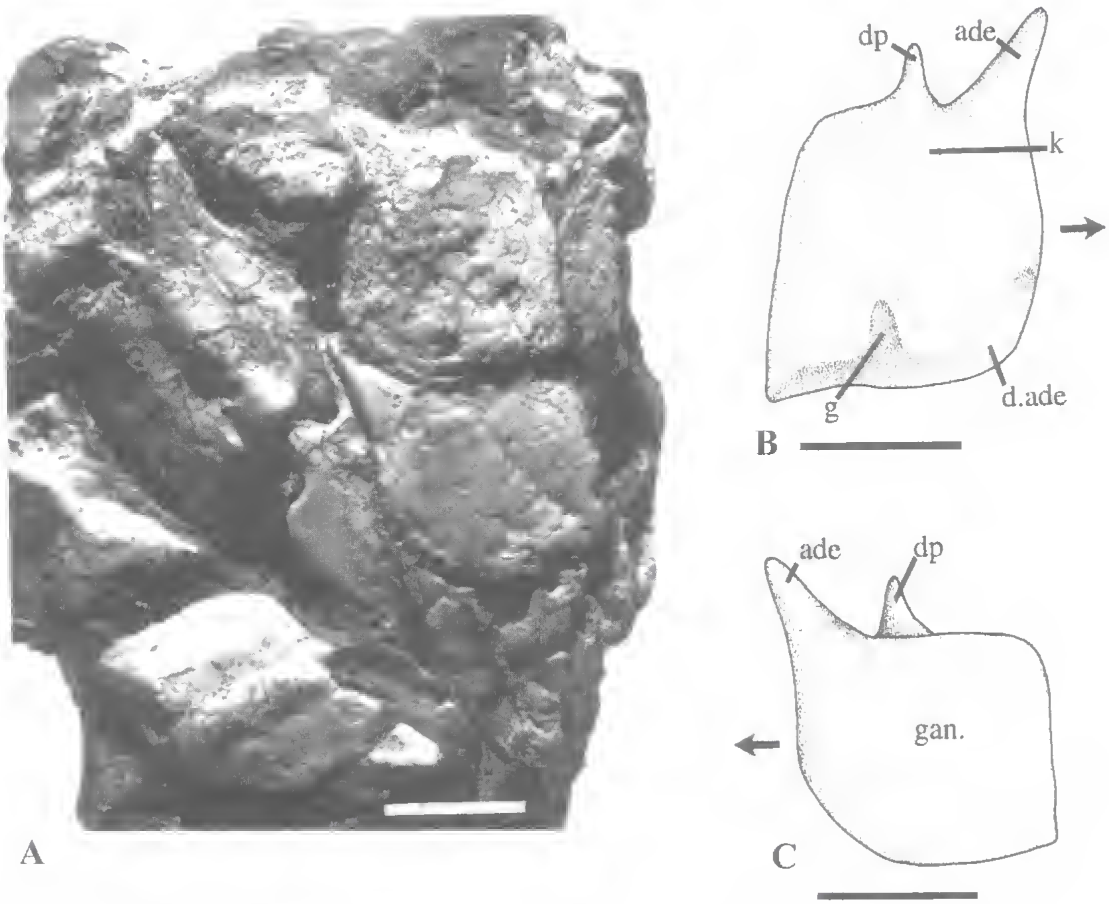

FIG. 4. Scale type 2, QMF35238, anterior - mid lateral scales, some of which remain in articulation. A, QMF35238; B, internal view of a single scale; C, external view of a single scale. ade = anterodorsal extension, d.ade = depression for the anterodorsal extension of the adjacent scale, dp = dorsal peg, g = groove, gan. = ganoine, k = keel. Arrow = anterior. Scalebar = 4mm.

low ridge crossing their external surface, indicating the position of the lateral line.

TYPE 6.

MATERIAL. QMF35242 (Fig. 8), incomplete scales scattered through a piece of consolidated red mudstone. Locality QML215.

Scale type 6 is known from a scattering of incomplete scales of which only the internal surface is exposed (Fig. 8). With no extension of the anterodorsal corner, the scales appear almost square and have a long, pointed peg with an opposing deep, triangular groove. A keel along the centre of the scale is present, but not pronounced. There are a number of small, regularly spaced, ventrally sloping projections along the posterior margin of the scale. One scale has at least 5 projections, but because the scales are incomplete it is difficult to know the number of projections that may have been present originally, or whether the number of projections varied between scales. The matrix also contains a large scale with a fold along the midline that may be an enlarged ridge scale from the dorsal or ventral margin of the tail.

COMPARISONS BETWEEN THE SCALES

Scale type 1 has a thin, delicate structure that distinguishes it from scales of type 2, which in contrast are robust with several clearly defined layers of ganoine. The rhombic shape of scale type 1 distinguishes it from scale types 4 and 6. The presence of a well-defined dorsal peg and an extended anterodorsal corner distinguish it from

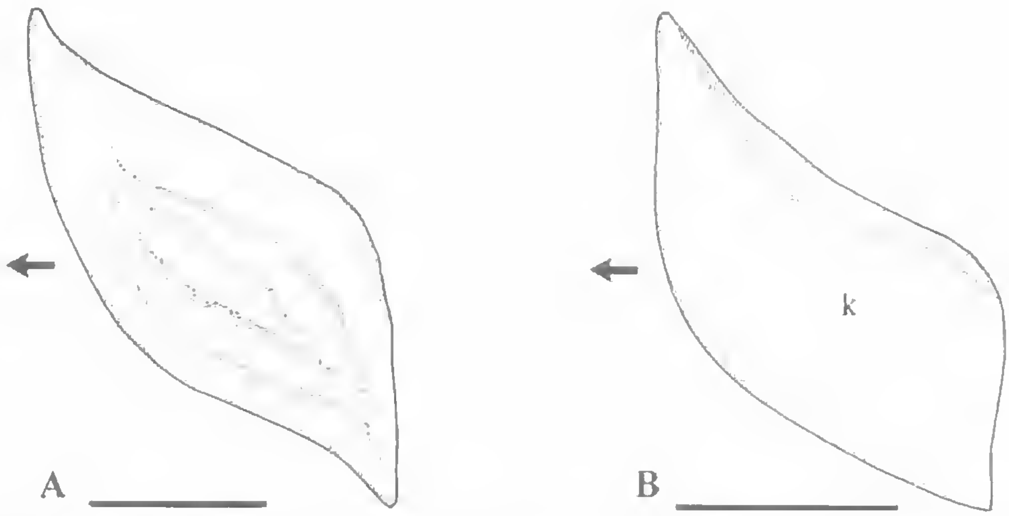

FIG. 5. Scale type 3. A = reconstruction of the external view of a posterior flank or caudal scale from QMF35239, showing the pattern of ornamentation. B = the internal surface of a complete scale from QM F35253, showing the keel. k = keel. Arrow = anterior. Scalebar = 1mm.

scale type 5 and the absence of ornamentation distinguish it from scale type 3.

Type 2 scales can be distinguished from the other Arcadia Formation scales by their larger size, more robust structure, their angular, rhomboid shape, and well developed peg-and-groove articulation.

Esin (1990) found that caudal scales were not useful taxonomically, but the presence of ornament on scale type 3 clearly distinguishes it from the rest of the Arcadia Formation actinopterygian scales, which are unornamented.

The height-length ratio of type 4 scales, in particular the lateral-line series, differentiates them from the other scale types.

Type 5 scales bear some similarity to the more dorsal or ventral scales of scale type 4, where the long body scales grade into more rhomboid scales. The height of the type 5 scales is slightly greater than their length as is the case in scales of type 4. The main difference between the scales of type 4 and type 5 lies in the morphology of the lateral-line scales. In type 4, the lateral line scales are elongate in comparison to the other body scales, whereas in type 5, the lateral line scales do not differ markedly in proportions from the other scales (Fig. 7). Type 5 scales may represent caudal or posterior body scales of the actinopterygian represented by type 4 scales, but it is more likely that differences in morphology of the lateral line scales indicate that type 4 and type 5 scales are from different actinopterygian taxa.

Scale type 6 may be differentiated from the other types of scales described above by its squarish shape, long pointed dorsal peg and deep triangular groove, reduced keel, absence of an extension of the anterodorsal corner, and a characteristic row of ventrally sloping projections along the posterior margin.

COMPARISONS WITH THE SCALES OF OTHER ACTINOPTERYGIANS

Dziewa (1977) noted that fish faunas from nonmarine environments are dominated by endemic forms. This means that the likelihood of finding actinopterygians with scales that are similar to those from the Arcadia Formation decreases with distance. Accordingly, I only reviewed descriptions of the scale morphology of Early Triassic non-marine actinopterygians from Gondwana.

The Arcadia Formation 'red beds' are typical of many Permian and Triassic deposits in that they show a taphonomic bias against fish and invertebrates while preserving the remains of tetrapods and coprolites in abundance. Fish are likewise rare in most of the other Australian Early Triassic deposits, with the exception of the Terrigal Formation (Gosford Subgroup, Narrabeen Group). This formation has yielded actinopterygian remains in abundance, particularly from the Railway Ballast Quarry and the Somersby Quarry, near Gosford in the Sydney Basin (Kemp, 1994; Ritchie, 1981, 1987; Wade, 1935,

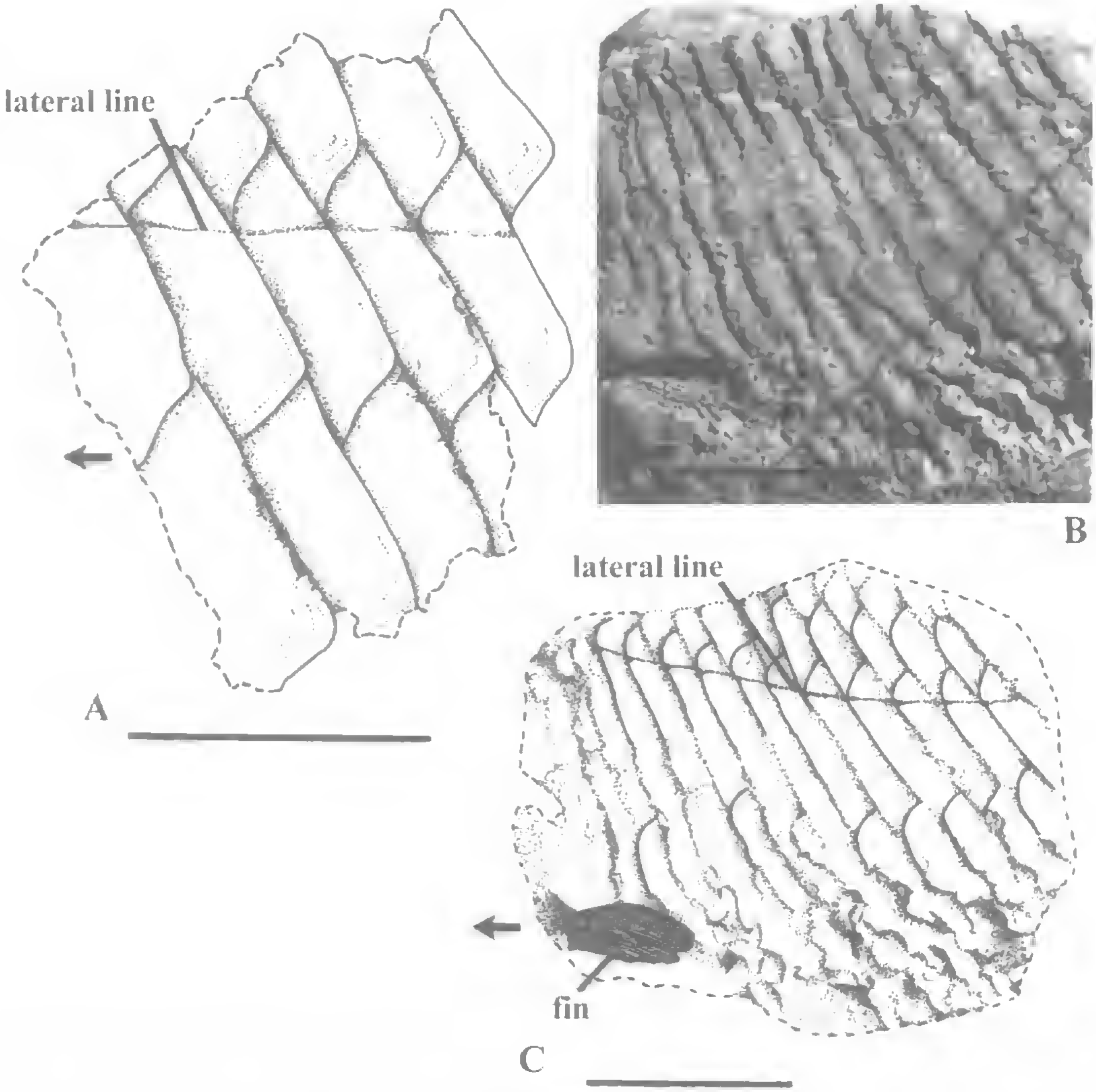

FIG. 6. Scale type 4, articulated scales from the mid body area including the lateral line series. A, reconstruction of QMF35240, showing position of the lateral line and pattern of imbrication; scalebar = 5mm. B, QMF35258, only an impression remains of the scales; scalebar = 5mm. C, QMF35258, showing the lateral line and the impression of a fin. Note the lateral line passes across the upper quarter of the scales in both specimens. Arrow = anterior.

1940; Woodward, 1890, 1908). Actinopterygians have also been described from the Knocklofty Formation in Tasmania (Banks et al., 1978; Dziewa, 1977, 1980; Johnston & Morton, 1890, 1891). Unfortunately, the taxonomic status of many Australian Triassic fish is uncertain because cranial regions are usually preserved poorly (Long, 1991).

Actinopterygians are also abundantly preserved in the Bekkers Kraal locality, Orange Free State, South Africa. Unfortunately, the Bekkers Kraal locality and the Gosford quarries are considered to be coeval with the South African Cynognathus Zone fauna and are thus younger than the Arcadia Formation. The Knocklofty Formation is the only Gondwanan deposit, contemporaneous with the Arcadia Formation, to have yielded some reasonably well preserved actinopterygian fossils.

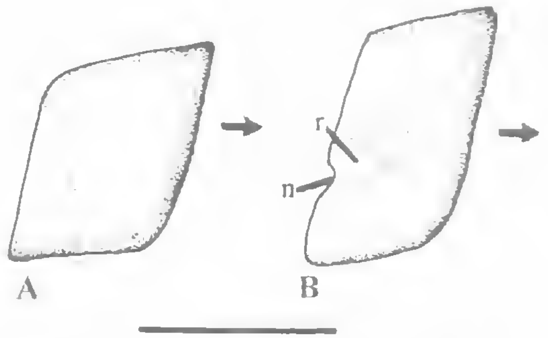

FIG. 7. Scale type 5, QMF35241, articulated mid-posterior flank scales, including the lateral line series. Diagrammatic representation of 2 scales: A, a scale from the series immediately above the lateral line; B, a lateral line scale. Note the characteristic notch in the posterior edge of the lateral line scale. n = notch, r = ridge along the lateral line. Arrow = anterior. Scalebar = 2mm.

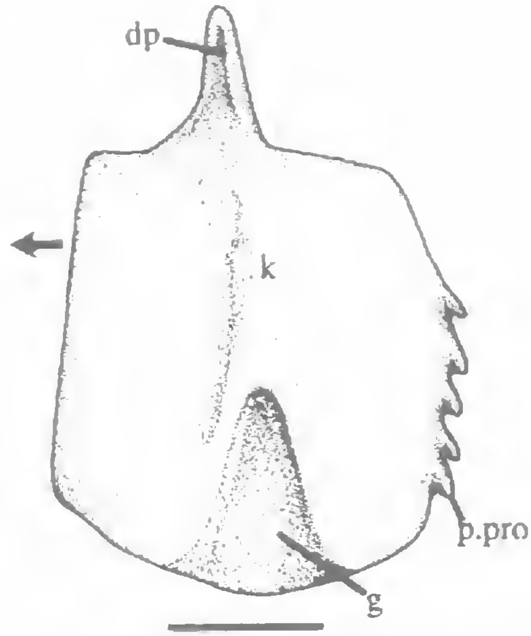

FIG. 8. Scale type 6, QMF35242, a composite reconstruction based on several incomplete anterior body scales. dp = dorsal peg, g = groove, k = keel, p.pro = posterior projections. Arrow = anterior. Scalebar = 1mm.

Scale types 1 and 2 show a very basic palaeoniscoid pattern that means they compare closely with the scales of many other actinopterygians. Because of this similarity they may not be attributed to any of the described Early Triassic fish.

A characteristic feature of scale type 3 is its ornament. In general, ornament is reduced on the posterior body scales of early actinopterygians and disappears from the caudal scales, but Esin (1990) noted that it remained visible in these areas in two species of *Acrolepis* (*A. rhombifera* and *A. macroderma*). In addition, ornament is present on the caudal scales of the two species of *Acrolepis* from Tasmania (*A. hamiltoni* and *A. tasmanicus*). According to the reconstruction and description provided by Dziewa (1977), the ridges on the scales of *Acrolepis* radiate from a single ruga on the posteroventral end of the scale (Fig. 9). Unfortunately, none of the scales on specimen QMF35239 are complete as most are missing their posterior edge (Fig. 5A), and it is not possible to determine whether their ridges radiate from a single ruga. The ornamentation on the scales of *Acrolepis* appears to differ somewhat from that of type 3 (QMF35239, Fig. 9; Fig. 5A, B).

Dziewa (1977) also noted that height never exceeds length in the scales of *Acrolepis*, and although most of the type 3 scales are greater in length than depth, the lateral line scales of QMF35239 are slightly greater in height than length. Height decreases relative to length toward the dorsal, ventral, and caudal body margins of *Acrolepis* (Dziewa, 1977, 1980), and in these areas, the scales are shaped much like those of type 3 (pers. obs.).

Scale type 3 is also similar in shape, size and ornamentation to the body scales of members of *Brookvalia*, being rhomboid with 3-4 rugae. Most of the members of *Brookvalia* had scales with 3 or fewer oblique ridges, although the Middle Triassic *B. latipennis* had up to 4 rugae (Wade, 1935; Hutchinson, 1973). A distinct difference between the scales of type 3 and those of *Brookvalia* is that, in those of *Brookvalia*, the ornamenting ridges run obliquely from the posterodorsal to the anteroventral corners, while in the type 3 scales the ridges are oriented obliquely anterodorsal to posteroventrally. Thus, the type 3 scales bear the closest resemblance to scales of *Acrolepis* and may represent a new species given its slight variation in ornamentation from those described previously.

In size, shape, and lack of ornamentation, the type 4 scales are similar to those of the perleidids, *Pristisomus gracilis* and *Tripelta dubia*, described by Woodward (1890) from the Terrigal Formation. Based on the position of the lateral line, which crosses obliquely the uppermost

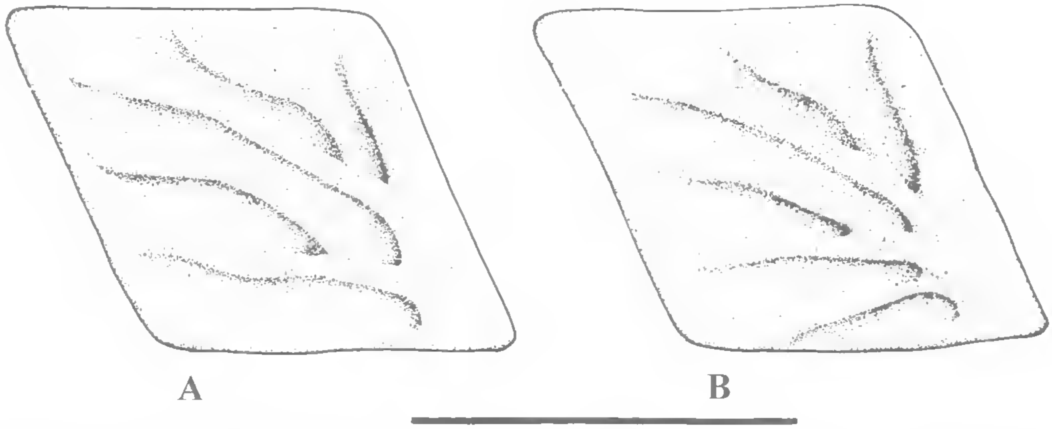

FIG. 9. Scales from the lateral line area of *Acrolepis hamiltoni* and *A. tasmanicus*, showing details of the ornamentation. Adapted from Dziewa (1977, fig. 11). A, *A. hamiltoni*, B, *A. tasmanicus*. Scalebar = 1mm.

quarter of the scale, scale type 4 is most similar to *P. gracilis*. In *T. dubia* the lateral line appears to pass through the midline of the scales (Woodward, 1890, Plate 6, fig. 4).

Turner (1982) reported the first actinopterygian, *Saurichthys* cf. *S. gigas* (Woodward, 1890), from the Arcadia Formation and suggested (pers. com. 1996) that scale type 4 might have belonged to this species. Material assigned to *Saurichthys* has been recovered from both QML78 and QML215, and includes a partial skull and a number of rostral fragments, some of which retain the lower jaws. An examination of the material led Dr A. Tintori (University of Milan) to regard it as the most primitive member of the genus (Turner, pers. com., 1996).

Saurichthys madagascariensis is the only saurichthyid described with a complete covering of body scales (Rieppel, 1980), this being regarded as a primitive character of *Saurichthys*. Other members of the genus have a reduced scalation consisting of 4 longitudinal rows of scales (Rieppel, 1980). The scales of *S. madagascariensis* are differentiated in shape and, with the exception of the elongated series, are ornamented characteristically with a shagreen of ganoine tubercles. The dorsal and ventral series consist of triangular scales that have a keel on the internal surface, posteriorly, which fits into a groove on the external surface at the anterior end of the succeeding scale. Immediately above the ventral series is a series of greatly elongated scales ornamented with dorsoventrally oriented ganoine ridges, rather than tubercles. Above this elongated series is a mid-lateral row of round-square shaped scales, above which was a series of slightly elongated rhomboidal scales, and two series of small rhombic scales, situated below the dorsal series of triangular scales. The type 4 scales bear no similarity to those of *S. madagascariensis* and it seems more likely that they belong to one or a number of different perleidids, similar to those described from the Terrigal Formation.

The lateral-line scales of type 5 are twice as deep as they are wide. In this sense they are similar to several of the Perleididae described by Woodward (1890) and later by Wade (1940) from the Terrigal Formation. Scales of *Chriotichthys gregarius* and *Zeuchthiscus australis* are also twice as deep as they are long; the depth of the scales of *Tripelta dubia* and *Pristisomus gracilis* is greater than double the length. Woodward (1890) noted that where the lateral line passes through the scales of *C. gregarius*, an external ridge is present. Although it is stated that the line crosses the scales near the dorsal edge, in two figured specimens the lateral line may be observed to cross the more posterior flank scales almost through the midline (Woodward, 1890, Plate 6, figs 6,7). Scale type 5 also shows a ridge along the lateral line which passes approximately through the middle of the scales. This ridge was not reported on the scales of *Z. australis* but Woodward (1890) did note that the lateral line was well marked. The scales of type 5 and those of *C. gregarius* are also similar in possessing thick unornamented scales with an extensive ganoine layer.

Scale type 6 must be the most distinctive of all the scale types recovered from the Arcadia Formation, yet none of the Early Triassic actinopterygians have comparable scales which are figured. A number of taxa from earlier and later periods had scales similar to type 6. Traquair (1877) figured a number of Carboniferous fish with scales similar in structure to type 6, most of which were from the family Elonichthyidae. Jubb & Gardiner (1975) assigned *Oxygnathus browni* Broom (1909) from the Cynognathus Zone of South Africa to *Elonichthys*, but did not figure its scales. In the original description of the specimen Broom (1909) described its anterior body scales as thin and ornamented with 8 or 9 irregular posteroventrally directed ridges. In many cases these ridges protrude beyond the posterior border of the scales and when viewed from the ventral surface appear similar to the projections on scale type 6. Schultze (1966) described and figured the scales of several species of *Pholidophorus* that are also similar, although this taxon is generally found in sites more recent than the Early Triassic.

Dicellopyge is another Early Triassic genus that might have had scales similar to those of type 6. Hutchinson (1975) reported that the scales of this genus had pectinated posterior edges, as do the type 6 scales. Unfortunately, the scales of *Dicellopyge* were not figured, and I have been unable to verify their similarity.

CONCLUSIONS

None of the scales described above are attributable to *Saurichthys* cf *S. gigas*, the only actinopterygian genus previously known from the Arcadia Formation. One of the scale types may belong to a new species of *Acrolepis* (Acrolepidae), 2 may be perleidids and 2 others are so generalised that they cannot be assigned to any of the known Triassic actinopterygians. Lastly, scale type 6, although distinctive, could not be compared with actinopterygians described as having similar scale morphology because their scales were not figured. Despite the taxonomic uncertainty, the scales provide evidence of at least 6 new taxa in the Arcadia Formation and increase the taxonomic diversity of the actinopterygian fauna from QML78 and QML215 significantly.

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